GENETIC DIFFERENTIATION IN SYMPATRIC BUT TEMPORALLY ISOLATED PINE BARK BUGS, ARADUS-CINNAMOMEUS (HETEROPTERA)

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Genetic differentiation in sympatric but temporally isolated pine bark bugs, *Aradus cinnamomeus* (Heteroptera)

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The pine bark bug *Aradus cinnamomeus* is a Eurasian insect pest of Scots pine. Each generation lives for two years in most areas in Europe, but in the north and in the Åland archipelago the generation time is three years. In western Finland, the 2-year bugs reproduce mainly in odd years, while in eastern Finland (as well as in eastern Sweden) the even-year generation predominates. Odd-year bugs are very rarely found in the even-year area, and even-year bugs are very rarely found within the odd-year area. The existence of sympatric but isolated alternate-year generations offers a possibility to study the effect of ecological genetic factors in a natural test situation since all environmental variables should be otherwise identical. In the north and in the Åland archipelago, the preponderance of one generation is not so pronounced, and three generations usually coexist in almost equal numbers.

The Finnish parapatric odd and even-year generations (which are in the majority) are genetically virtually identical, while the odd and even-year minority generations deviate genetically (and morphologically) from the majority ones. In the three-year area the sympatric but allochronic bug generations differ genetically from each other to about the same extent as the allopatric but synchronic populations differ from each other. The sympatric differentiation can be explained as being a result of within species competition, although several other possible explanations exist. Furthermore, the two-year bugs collected from eastern Sweden appeared to diverge genetically, although they represent the locally predominating generation.

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The pine bark bug, *Aradus cinnamomeus* Panzer, is a widely distributed heteropterous pest of young Scots pines, *Pinus sylvestris* (L.). During recent decades the bug has increased in abundance and become a serious pest in Europe and Siberia (TURCEK 1964; BRAMMANIS 1975; DOOM 1981; HELIÖVAARA and VÄISÄNEN 1983). Hundreds or even thousands of bugs can be found on a single stem in open, dry heath forests. Both adults and larvae live in the crevices of the bark, and suck the sap of pine saplings. The life cycle of this hemimetabolous insect takes two years, with two obligatory hibernations in most parts of Europe including southern Finland. However, in the north and in the Åland archipelago the life cycle takes three years (BRAMMANIS 1975: HELIÖVAARA and VÄISÄNEN 1987).

The distribution of the two-year bugs in the southern half of Finland follows an exceptional pattern: There are two alternate-year generations which live almost exclusively in different geographical areas. In eastern Finland the bugs reproduce in even years, and in western Finland they reproduce in odd years. The two generations border each other along a narrow zone of overlap (about 3.5 km), where both even and odd-year bugs are found in about equal numbers, and even on the same trunks (for details of the location and structure of the transition zone, see HELIÖVAARA and VÄISÄNEN 1984a, b, 1987, and Fig. 1). Interestingly, very few odd-year individuals can be found within the even-year generation of eastern Finland; respectively, very few even-year individuals occur within the western odd-year generation. We found 25 adults among 36,000 larvae in one (even-year) and 34 adults among 54,000 larvae in another (odd-year) generation; that is, these minority individuals are present at concentrations of less than one per thousand.

None of the three local generations exclusively

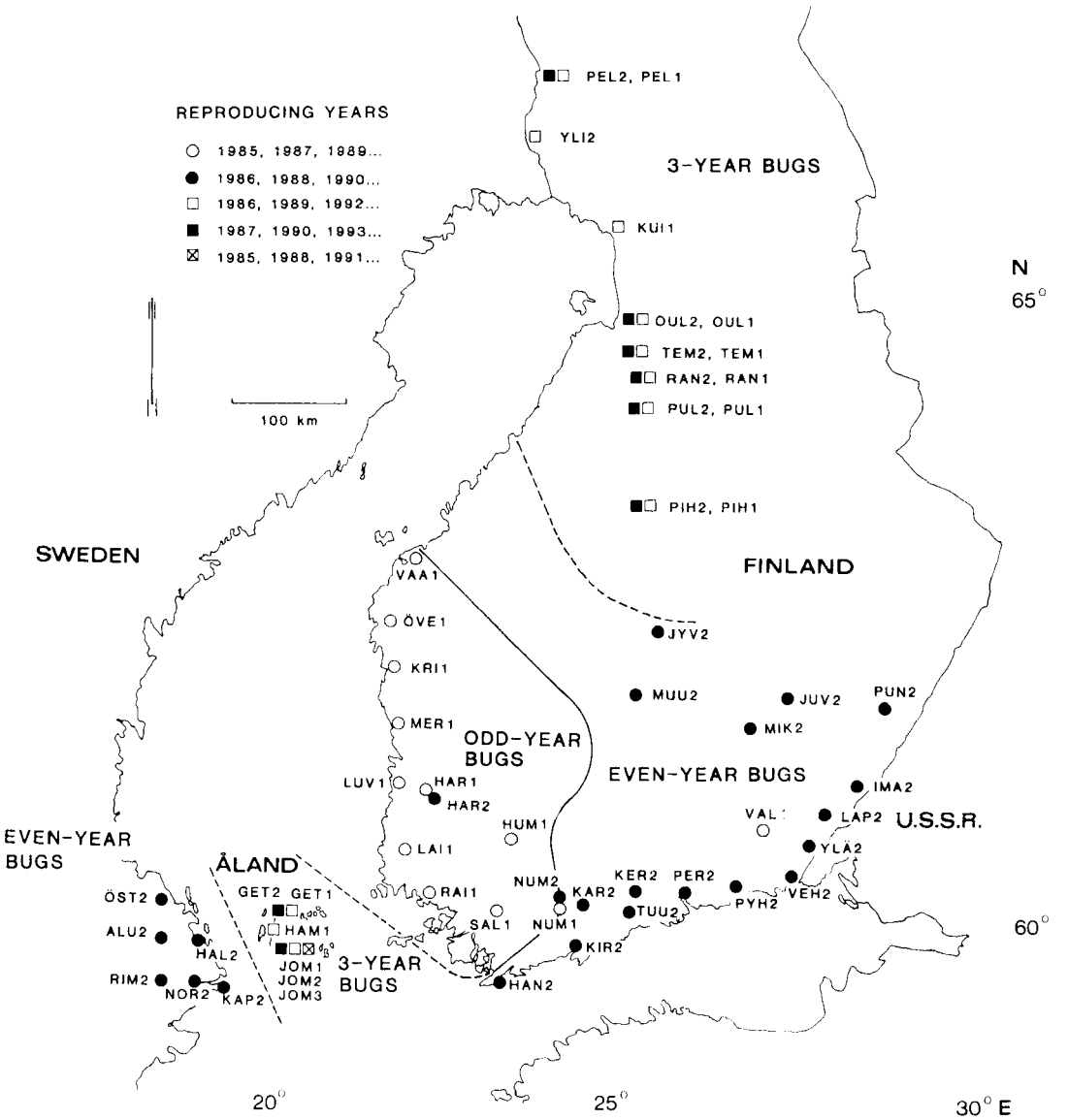

Fig. 1. Sampling sites and the geographical distribution of the even-year, odd-year and 3-year populations of *Aradus cinnamomeus* in Finland, including the Åland archipelago, and eastern Sweden.

predominates in the north and in the Åland archipelago, where the life cycle is three years, but instead there is a mosaic of spatially variable preponderance relationships. The preponderance seems to be seldom, if ever, as total as is normally the case in the two-year areas. The life cycle again takes two years in eastern Sweden, and the even-year generation shows an absolute majority in the same way as in eastern Finland (HELIÖVAARA and VÄISÄNEN 1987).

The sympatric but temporally separated generations of *A. cinnamomeus* are reproductively isolated from each other, and function as separate ecological and evolutionary entities. Even though all age-classes are uniformly distributed along the pine trunk, and they seem to exploit the same resources,

the niche overlap between the coexisting age-classes may not be total (HELIÖVAARA and VÄISÄNEN 1986). On the basis of field experiments into crowding, transplantation and mixing the locally predominating generations from eastern and western Finland, we have concluded that within-species interference competition can reasonably well explain the parapatry of the temporally separated majority generations. The inferred effect of interference competition is reinforced by within-species exploitation competition and parasitization by a scelionid wasp *Telenomus aradi* Kozlov (HELIÖVAARA and VÄISÄNEN 1986).

The existence of reproductively isolated but sympatric generations offers a possibility to study the effect of ecological genetic factors in a natural test situation where all environmental variables should be identical. There are two levels of sympatry among the two-year bugs: sympatry in the transition zone between the allochronic eastern and western majority generations, and sympatry of the local minority and majority generations both in the east and west. Before this study, it was not definitely known whether the two parapatric and temporally separated majority generations really belonged to the same species. The presence of a scarce minority among majority generations evoked several questions. Where these dissenters evolutionary units of their own, or did they simply belong to one or another majority generation? Could they be sporadic airborne individuals from the synchronic allopatric majority generation? Or, perhaps local individuals with accelerated or delayed development (cf. LLOYD and DYBAS 1966)? Still less was known about the three-year populations. Do the three-year populations differ from the two-year populations? Are the sympatric three-year generations more similar than the allopatric ones?

We approached these problems by using routine enzyme electrophoresis. The genetic distance between populations should provide answers to the questions posed above. They may also show the possible reciprocal effects of temporally isolated bugs on each other.

Material and methods

Two-year bugs. — Between twenty and eighty adult individuals, mostly females, were sampled at each of the localities shown on the map (Fig. 1) and in Table 1. The eastern, even-year dominating generation was sampled in the southern half of Finland mainly in May–June, 1984, and the western, odd-year dominating generation in August–September, 1984. The very scarce eastern odd-year generation (VAL1) was sampled at the same time as the western odd-year majority generation; and the scarce western even-year generation (HAR2) simultaneously with the eastern even-year generation. Additional samples were taken of the predominating even-year populations in Finland in August, and in eastern Sweden in October, 1985.

Three-year bugs. — Sampling was carried out in the same way as in the case of the two-year bugs, except that IV-instar larvae were also used as well as adults. In preliminary tests no difference was found between adults and IV-instar larvae with respect to the electrophoretic findings. Three-year bugs were sampled in northern Finland in August, 1985, and in the Åland archipelago in August, 1984, and September–October, 1985 (Fig. 1, Table 1).

Electrophoresis. — Bug samples taken from different sites were subjected to routine starch gel electrophoresis and enzyme assays. Ten loci were followed. The genetic distances between bugs from different localities were calculated, on the basis of electrophoretic variation, according to NEI (1978). The distances are shown in the form of a UPGMA dendrogram.

The body length of Finnish two-year individuals was measured for preliminary morphometric analysis.

Results

Aradus cinnamomeus proved to be a highly invariable insect species as regards the enzyme loci examined (Table 1). Variation was confined to the *Isocitrate dehydrogenase, Peptidase-1* and *Phosphoglucomutase* loci. Only a few variants were detected in the other seven enzyme systems studied. Owing to the low variation, the distances shown in the dendrogram are very short (Fig. 2). More than 70 % of the samples belonged to the six lowest branches of the UPGMA dendrogram, deviating from each other by a genetic distance of less than 0.0025.

The two widely distributed parapatric alternate-year majority generations (even-year generation in the east and odd-year generation in the west) in Finland are genetically completely or almost identical (for the only exceptions, KER2 and JYV2, see below). Single heterozygous individuals account for

Table 1. Sample codes, sampling sites with their coordinates according to the Finnish uniform grid (27°E) system, sampling dates, number of individuals electrophoresed (N) and their developmental stage (S; A = adult, L = IV instar larva), average heterozygosity (H; Hardy-Weinberg expected), and polymorphic loci

Code	Locality	Grid	Date	N	S	H	Polymorphic loci
Eastern Finnish odd-year minority generation:							
VAL1	Valkeala	675:48	20.IX.1984	10	A	0.035	*Idh*
Western Finnish odd-year majority generation:							
VAA1	Vaasa	700:23	17.VIII.1984	20	A	0.006	*Pgm*
ÖVE1	Övermark	695:21	17.VIII.1984	20	A	0.000	–
KRI1	Kristiinankaupunki	692:20	17.VIII.1984	20	A	0.024	*Pgm*
MER1	Merikarvia	687:21	17.VIII.1984	22	A	0.000	–
LUV1	Luvia	681:21	17.VIII.1984	23	A	0.006	*Pgm*
HAR1	Harjavalta	680:24	4.IX.1984	28	A	0.000	–
LAI1	Laitila	676:21	17.VIII.1984	23	A	0.024	*Mdh-II*
HUM1	Humppila	676:30	4.IX.1984	17	A	0.000	–
RAI1	Raisio	672:23	15.VIII.1984	23	A	0.000	–
SAL1	Salo	670:28	4.IX.1984	21	A	0.012	*Idh, Pgm*
NUM1	Nummi-Pusula	673:32	4.IX.1984	16	A	0.017	*Pgm*
Western Finnish even-year minority generation:							
HAR2	Harjavalta	680:24	29.V.1984	20	A	0.049	*Idh, Pgm, Pep-1*
Eastern Finnish even-year majority generation:							
NUM2	Nummi-Pusula	673:32	28.V.1984	39	A	0.052	*Idh, Pgm, Pep-1*
KAR2	Karkkila	671:34	28.V.1984	62	A	0.006	*Idh, Pgm, Pep-1*
HAN2	Hanko	664:28	12.VI.1984	22	A	0.000	–
KIR2	Kirkkonummi	666:35	12.VI.1984	27	A	0.000	–
TUU2	Tuusula	669:38	17.VI.1984	21	A	0.006	*Pgm*
KER2	Kerava	670:39	6.VI.1984	22	A	0.044	*Pgm, Pep-1*
PER2	Pernaja	670:44	5.VI.1984	22	A	0.006	*Pgm*
PYH2	Pyhtää	670:47	5.VI.1984	21	A	0.006	*Pgm*
VEH2	Vehkalahti	671:51	5.VI.1984	21	A	0.013	*Pgm*
YLÄ2	Ylämaa	674:55	5.VI.1984	22	A	0.000	–
LAP2	Lappeenranta	677:56	5.VI.1984	22	A	0.016	*Pgm*
IMA2	Imatra	678:59	5.VI.1984	21	A	0.027	*Pgm*
MIK2	Mikkeli	684:51	6.VI.1984	21	A	0.012	*Pgm*
PUN2	Punkaharju	685:62	5.VI.1984	21	A	0.018	*Pgm*
JUV2	Juva	686:54	6.VI.1984	22	A	0.006	*Pgm*
MUU2	Muurame	689:43	20.VIII.1985	82	A	0.019	*Pep-1*
JYV2	Jyväskylä	691:43	20.VIII.1985	51	A	0.038	*Mdh-II, Pgm, Pep-1*

the few differences found. The scarce two-year minority generations from Harjavalta (HAR2) and Valkeala (VAL1) deviate clearly from the general majority pattern. The statistical probability is small that the observed result (2 of the 2 minority samples deviating, 24 of the 26 majority samples non-deviating) is due to chance (Fisher's exact test, $p=0.016$; KER2 and JYV2 included, NUM1, NUM2, and the Swedish samples omitted from the analysis).

Samples taken from the narrow transition zone between the parapatric alternate-year majority generations show a pattern in which one generation (NUM1) conforms to the majority generation pattern and is genetically completely or almost identical with it. However, the other generation in the transition zone (NUM2) is genetically similar to the minority sample (HAR2) lying far away from the transition zone.

Samples taken in Kerava (KER2) and Jyväskylä (JYV2) are exceptional since they belong to the eastern even-year generation, but differ genetically from the other majority samples from eastern Finland. In both cases the predominance of the majority generation is, however, more or less decreased. While the proportion of the minority generation is normally less than 0.1 %, it is about 10 % or more in these exceptional cases. The sample JYV2 had been collected near the transition zone between the two-year and three-year bug populations in the north, where the predominance relationships of the allochronic generations are rather complicated (HELIÖVAARA and VÄISÄNEN 1987). The sample KER2 had been collected from a small area with unusual predominance relationships (HELIÖVAARA and VÄISÄNEN, unpubl.), which may be due to human activity such as the establishment of pine plantations

(*Table 1, cont.*)

Code	Locality	Grid	Date	N	S	H	Polymorphic loci
Eastern Swedish even-year majority generation:							
KAP2	Kapelskär		2.X.1985	49	A	0.031	*Pep-1*
NOR2	Norrtälje		2.X.1985	56	A	0.092	*Pgm, Pep-1*
RIM2	W of Rimbo		2.X.1984	47	A	0.035	*Pep-1*
HAL2	Hallstavik		2.X.1985	41	A	0.053	*Pgm, Pep-1*
ALU2	Alunda		2.X.1985	40	A	0.024	*Idh, Pgm, Pep-1*
ÖST2	N of Östhammar		2.X.1985	46	A	0.058	*Pgm, Pep-1*
Northern Finnish three-year generations reproducing in 1986, 1989, etc.:							
PIH1	Pihtipudas	703:43	23.VIII.1985	68	A	0.013	*Pgm, Pep-1*
PUL1	Pulkkila	713:44	23.VIII.1985	32	A	0.012	*Pgm, Pep-1*
RAN1	Rantsila	715:43	23.VIII.1985	10	A	0.000	–
TEM1	Temmes	717:43	23.VIII.1985	37	A	0.000	–
OUL1	Oulu	721:42	23.VIII.1985	67	A	0.032	*Pgm, Pep-1*
KUI1	Kuivaniemi	728:41	22.VIII.1985	7	A	0.042	*Pep-1*
PEL1	Pello	741:36	22.VIII.1985	12	A	0.000	–
Three-year generation in the Åland archipelago, reproducing in 1986, 1989, etc.:							
JOM1	Jomala	668:10	30.IX.1985	37	A	0.018	*Pep-1*
HAM1	Hammarland	670:09	1.X.1985	30	A	0.038	*Pgm*
GET1	Geta	671:10	1.X.1985	34	A	0.009	*Pep-1*
Northern Finnish three-year generation, reproducing in 1987, 1989, etc.:							
PIH2	Pihtipudas	703:43	23.VIII.1985	22	L	0.000	–
PUL2	Pulkkila	713:44	23.VIII.1984	19	L	0.000	–
RAN2	Rantsila	715:43	23.VIII.1985	6	L	0.000	–
TEM2	Temmes	717:43	23.VIII.1985	37	L	0.000	–
OUL2	Oulu	721:42	23.VIII.1985	74	L	0.002	*Pgm*
YLI2	Ylitornio	736:35	22.VIII.1985	30	L	0.000	–
PEL2	Pello	741:36	22.VIII.1985	22	L	0.000	–
Three-year generation in the Åland archipelago, reproducing in 1987, 1990, etc.:							
JOM2	Jomala	668:10	30.IX.1985	18	L	0.011	*Mdh-II*
GET2	Geta	671:10	1.X.1985	39	L	0.009	*Pep-1*
Three-year generation in the Åland archipelago, reproducing in 1985, 1988, etc.:							
JOM3	Jomala	668:10	16.VIII.1984	14	A	0.041	*Pgm, Pep-1*

and the mixing of samplings of different origin at the nearby forest tree breeding station. If KER2 and JYV2 are omitted from the analysis of the Finnish two-year minority and majority pattern, the statistical probability of the observed pattern (2 of the 2 minority samples deviating, 24 of the 24 majority populations non-deviating) being due to chance would be even smaller (Fisher's exact test, $p=0.003$).

Individuals of the genetically deviating samples collected at two sample sites (HAR1, HAR2 and NUM1, NUM2) were shorter, measured as total adult length. The correlation was statistically significant ($p<0.001$ and $p<0.05$, respectively). The genetic distance between the generations at these two sites was due to the *Peptidase-1* locus. At the sample site VAL1, no morphological deviation from the "normal" individuals was observed; the genetic distance was due to variation at the *Isocitrate dehydrogenase* locus. We assumed that the majority population here would be similar to that at the nearby localities (LAP2, YLÄ2) on the Salpausselkä esker ridge and elsewhere in eastern Finland.

The two-year pattern in Sweden seems to be quite different from that in Finland. Only one sample (ALU2) out of six belonged to the genetic types prevailing in Finland. If these samples are included in the statistical analysis of the two-year bugs, the probability that the result (2 of the 2 minority samples deviating, 25 of the 32 majority samples non-deviating) being due to chance is 0.064 (Fisher's exact test; all two-year samples included except NUM1 and NUM2).

Most of the three-year bug samples appeared to be genetically similar to two-year samples, belonging to the five lowest branches of the UPGMA

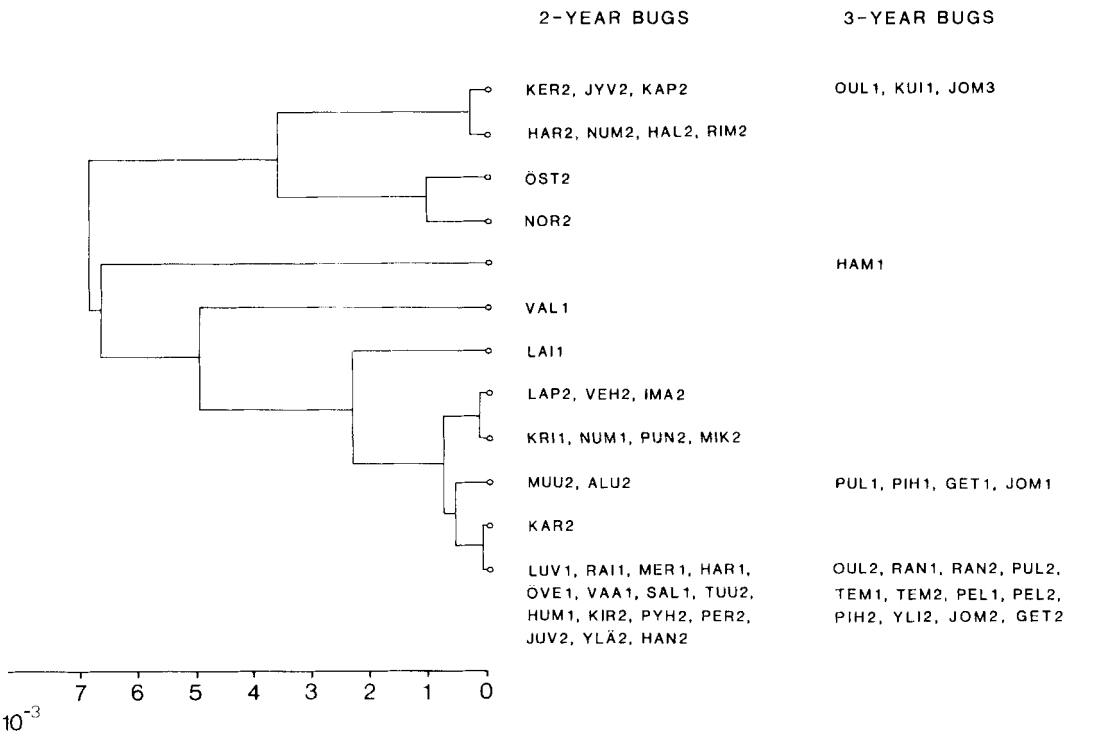

Fig. 2. A UPGMA dendrogram showing the genetic differences between *Aradus* populations. The codes refer to sampling sites (Fig. 1, Table 1).

dendrogram (Fig. 2). The results show no distinct biogeographic pattern as regards the genetic variation among the three-year bugs. The small number of samples that deviated more originated from northern Finland (OUL1, KUI1) and the Åland archipelago (JOM3, HAM1). The sympatric allochronic generations were genetically different (genetic distance more than 0.0005) from each other in several cases (OUL1, OUL2; JOM1, JOM2, JOM3; PUL1, PUL2; PIH1, PIH2; GET1, GET2). The sympatric but allochronic generations were as frequently similar to each other as were synchronic but allopatric bug populations (2×2 contingency table test; A. genetic distance between similar samples = 0, $\chi^2=0.13$, N.S.; B. genetic distance between similar samples less than 0.0005, $\chi^2=0.18$, N.S.).

Discussion

The results show that sympatric but allochronic pine bark bugs often differ from each other genetically. The minority generations among the two-year majority generations are not sporadic airborne individuals from one or another of the majority generations, or local individuals with accelerated or delayed development, since they differ genetically from both of the majorities, while these parapatric and temporally separated majority generations are virtually identical. The fact that the sympatric populations are genetically different suggests that temporal isolation between the alternate-year populations results in practically complete reproductive isolation. This could hypothetically give rise to sympatric speciation (Maynard Smith 1966; Felsenstein 1981). However, in tne case of the pine bark bug it has been reported that a possible break-down mechanism of reproductive isolation between allochronic alternate-year bugs takes place via mutual contact with the three-year bug populations (Heliövaara and Väisänen 1987).

The sympatric differentiation is also often evident in the three-year bug samples, although there the general pattern seems to be more random, the deviating generation(s) being different in different places. This conforms to the spatially and perhaps

also temporally varying mosaic-like pattern of the predominance relationships in the three-year bugs (HELIÖVAARA and VÄISÄNEN 1987).

What is biologically more interesting than the sympatric differentiation itself, is the curious way in which the two-year bugs genetically differ from each other. The similarity between the allopatric (or parapatric) allochronic majority populations and, on the other hand, the difference between the sympatric but allochronic minority populations would suggest that ecological character displacement could be a plausible hypothesis to explain the observed pattern. Although the term character displacement was originally restricted to cases in which two closely related species have overlapping ranges (BROWN and WILSON 1956; see also GRANT 1972), it can be suggested that the term should be widened to cover within-species cases as well.

Next, we consider in more detail the possibility that intraspecific character displacement is involved in our single species system. The evolutionary units here are not closely related species, but temporally isolated populations of a single species. Sympatry and allopatry are not absolute concepts, but dependent on the relative densities and predominance relationships of the different generations. The two alternate-year generations are actually sympatric everywhere, but due to the overwhelming differences in abundance, the pattern seems to be similar to that of classical cases with allopatric and sympatric populations. In addition, our data are not based on ordinary morphological but genetic character states.

We suggest that the results of the present study can be interpreted to reflect the following evolutionary processes in the Finnish two-year pine bark bugs (see Fig. 3):

1. *Pre-contact.* — We consider it very probable that the pre-contact character state of the allopatric and allochronic bug populations has been the common gene pool of the majority generations (i.e., the five lowest branches in the UPGMA dendrogram, Fig. 2). Both the allopatric asynchronic majority generations, the even-year generation in the east and the odd-year generation in the west, are similar and genetically almost invariable. Deviations from this pattern are fortuitous, and their relative frequency is very small.

2. *Contact.* — The two majority generations are in spatial contact in the transition zone, which is the area where neither of these units predominates. Here one or other of these competitive units may begin genetic divergence. Evidence for such character displacement has been observed at Nummi-Pusula (NUM1 vs. NUM2).

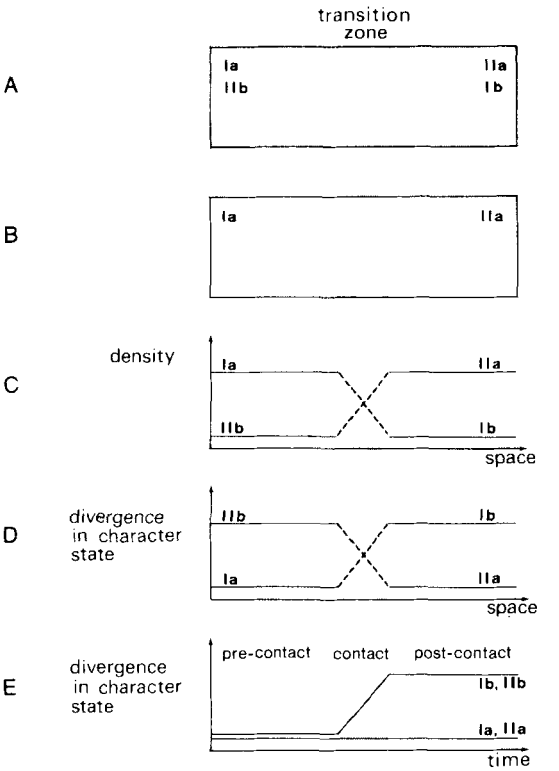

Fig. 3. A hypothetical model for possible ecological character displacement in alternate-year generations of *Aradus cinnamomeus*. Abbreviations: Ia—western odd-year majority generation, IIa—eastern even-year majority generation, Ib—eastern odd-year minority generation, IIb—western even-year generation.

A. Geographical distributions of the alternate-year generations
B. Distributions of the majority generations Ia and IIa
C. Relative densities of the bug generations
D. Character displacement in space
E. Character displacement in time

3. *Post-contact.* When one generation almost exclusively predominates locally, the other diverges (unilateral character displacement). This has been observed in both generations and in two different areas (HAR2 vs. western odd-year generation, VAL1 vs. eastern even-year generation; however, note that the divergence is due to allelic changes at different loci).

It is usually difficult to infer the pre-contact character state in cases supposed to be due to character dis-

placement. In the present single species system, the original character seems to be easily detectable owing to the genetic and ecological similarity of the two allopatric predominating evolutionary units. The assumption that no factors other than ecological character displacement influence the differences in character state between locations may often be false (GRANT 1972, 1975; ARTHUR 1982; SCHLUTER et al. 1985). In the present study, most of the other factors (except chance) are apparently eliminated. The definition of the similarity between two species may involve serious difficulties in the study of character displacement, but such difficulties do not exist in the present case.

However, it should be stressed that the above explanation is not necessarily the only reasonable one. For example, the divergence in the small minority populations might be due to genetic drift. Genetic drift may be a plausible explanation especially in the case of VAL1, where the divergence was due to variation in the *Isocitrate dehydrogenase* locus. Drift might also explain the divergence in the three-year populations and in the Swedish populations. On the other hand, the minority, three-year, or Swedish populations are not particularly small compared to the majority populations in certain localities in southern Finland.

There are also some limitations and contradictions in our data that go against the above explanation (i.e., character displacement). First of all, the genetic distances determined, using the present electrophoretic methods, are relatively small. In this study only a few samples of the two-year minority bug generations were examined because of difficulties in collecting these extremely scarce individuals. Moreover, the Swedish samples do not conform to the Finnish majority generation pattern. However, this may be easily explained as being due to the disjunct distribution. In eastern Sweden, the local distribution is also very scattered, the small pine stands infested by the bug being separated by wide belts of deciduous forests and fields. In southern Finland, on the other hand, the distribution of the bug is virtually continuous (HELIÖVAARA and VÄISÄNEN 1984a, 1987). Thus, taking these limitations of the present material and methods into account, far-reaching conclusions can be misleading without the development of more efficient methods and a more thorough examination of enzymatic variation in the pine bark bug.

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